J. A. Moy-Thomas and his association with the British Museum (Natural History)

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Introduction

The British Museum (Natural History), as a national institution for the repository and care of natural history specimens and furtherance of their understanding, owes its efficiency not only to those employed there but also to that very large body of dedicated amateurs and professional scientists who collect, donate and work on the collections. Over the last hundred years their contributions have been very significant and there has been a history of close collaboration. For instance, Richard Lydekker (1849–1915), who worked for the Indian Geological Survey, compiled the catalogues of the Museum's collections of fossil mammals, reptiles and birds. A. W. Wrigley (1885–1953), a draughtsman, worked closely with Museum staff to produce many papers on Tertiary molluscs and Eocene foraminifera.

It seems appropriate in this, the Museum's centenary year, to acknowledge the contributions made by our non-Museum colleagues. One such was J. A. Moy-Thomas, who was closely associated with the fish section immediately prior to the second world war. His association with the Museum was unfortunately brief, but during those few years he collected and examined a variety of interesting fossil fishes in our collections and, above all, typified that essential collaboration between Museum staff and others which has so often proved rewarding.

J. A. Moy-Thomas

James Moy-Thomas, eldest son of Mr and Mrs Alan Moy-Thomas, was born in 1908. Billy, as he was affectionately known, was sent to Harrow from whence he obtained an open scholarship to Christ Church, Oxford. After three years of study he was awarded a first class honours degree in zoology in 1930. The following session he remained up at Oxford and attended classes in geology. For most of this period his tutor was Dr G. de Beer, with whom he was later to form a close friendship. In the summer of 1932 at the instigation of de Beer he visited the Zoology Department of the University of Glasgow. There he enjoyed the hospitality of Professor Graham Kerr and was encouraged to re-examine developmental stages of *Polypterus*, making use of the specimens brought back by the late John Samuel Budgett, including the material used by Kerr himself in 1907. Moy-Thomas's work on *Polypterus* was published in 1934. In the meantime he worked as an assistant to Professor Walter Garstang at Leeds where he met and married Miss Joy Mitchell.

This period also saw the publication of his first paper, in collaboration with T. H. Harrison of Pembroke College. It consisted of a short note to *Nature* on the St Kilda house mouse. Two more papers followed in 1933 and in the ensuing years he published a further 34 papers. He returned to Oxford in the summer of 1933 to the post of University demonstrator in the Department of Zoology and Comparative Anatomy. This was in essence

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a research fellowship and in his first year back at Oxford J. A. Moy-Thomas attended various lecture courses, including those of Mr J. Z. Young who was later to become a close friend. During the next seven years he also became a good friend and colleague of Dr E. I. White of the British Museum (Natural History), and they both frequently attended meetings of the newly-formed Tetrapods Club (a dining club in London, founded in 1930 for those interested in vertebrate zoology). E. I. White introduced him to Sir Arthur Smith-Woodward (erstwhile keeper of the Department of Geology) who in 1935 gave Moy-Thomas permission to use his many unpublished notes on fossil fishes.

In 1936 Moy-Thomas shared the Rolleston Memorial Prize with B. G. Maegraith (a fellow of Exeter College) and in the following year he was re-elected to the post of University Demonstrator and lecturer. Shortly afterwards he became the first holder of the E. T. Browne Fellowship at Queen's College.

In each of the years 1935, 1937, 1938 and 1940 he received small sums of money from the Godman Exploration Fund (£20 in 1935, £30 in the subsequent years) to enable him to collect fossils for the British Museum (Natural History). He was a diligent collector with infinite patience who furnished the Museum with some 127 specimens of fossil fishes (49 in counterpart), mainly from Glencartholm, only 9 of which were purchased. On many of his collecting trips he was accompanied by his wife but at Glencartholm in 1933 he was helped by Mr W. S. Bullough (later Professor of Zoology at Birkbeck College, London). Ironically it was Bullough who found the specimens of *Tarrasius* on which Moy-Thomas's 1934 Zoological Society paper was based.

In 1939 Moy-Thomas joined the English–Norwegian–Swedish (E.N.S.) expedition to Spitzbergen (not Greenland as is erroneously reported in his obituary notices) which was the result of an intimate collaboration between the British Museum (Natural History), the Paleozoological Department of the Riksmuseum in Stockholm and the Paleontological Museum in Oslo (Fig. 1). The initiator was Professor E. A. Stensiö and the expedition was financed by all three countries. The English members were Dr E. I. White, J. A. Moy-Thomas, J. Brough and W. N. Croft. The Norwegians were Professor A. Heintz, Sven Føyn and the student Aarhus. The Swedish members were Professor E. A. Stensiö, leader of the expedition, E. Jarvik and G. Wängsjö, and they were accompanied by Dr N. Della of Riga.

At the beginning of the war Moy-Thomas started in the intelligence service but soon volunteered for flying work. Having successfully completed his tour of operations as a night fighter observer/navigator he was posted to R.A.F. Defford which was a non-operational unit concerned with the development and pre-service testing of air interception apparatus (airborne radar). This apparatus was being developed by the Telecommunication Research Establishment (T.R.E. Malvern). Here, together with Professor Derek Jackson F.R.S. (Spectroscopy, Oxford), he flew as a radar observer in Mosquitoes and Beaufighters. Moy-Thomas was killed in a motor accident while on duty on February 29, 1944.

He was a sociable person with a great gaiety, sense of humour and zest for life. Everyone with whom he came into contact seems to have liked him. He was a very good golfer (handicap 3), enjoyed a game of darts and was an avid stamp collector. At Oxford he is remembered as a most successful teacher and tutor and at the British Museum (Natural History) as an endearing character with a sense of humour and a first-class memory. He greatly admired both Professors W. Garstang and E. S. Goodrich and for the latter he erected the genus *Goodrichia* (a large shark from Glencartholm) in 1936. The name was unfortunately pre-occupied (by a mollusc) and it was subsequently changed posthumously to *Goodrichichthys* (Moy-Thomas, 1951).

During his short career J. A. Moy-Thomas worked mainly on fossil fishes (32 papers), particularly shark-like forms and palaeoniscids. However, he still found time for experimental work and as late as 1940 was examining the dermal bones of the skull of the trout in an effort to determine whether or not their development was influenced by the neuromast organs. Although one of his longest papers was on coelacanths perhaps his most notable was on *Palaeospondylus*.

Fig. 1 J. A. Moy-Thomas (left) shown here with W. N. Croft (1915–1953, a palaeobotanist in the British Museum (Natural History)) during the English–Norwegian–Swedish expedition to Spitzbergen (1939). Croft, like Moy-Thomas, died at a young age. He collected a large number of Old Red Sandstone fishes and Devonian plants for the Museum.

Interpretation of *Palaeospondylus*

Genus *PALAEOSPONDYLUS* Traquair, 1890
Fig. 2A– C

TYPE SPECIES. *P. gunni* Traquair, 1890.

Towards the end of his short career Moy-Thomas turned his attention to *Palaeospondylus gunni* Traquair, an enigmatic fossil from the Middle Old Red Sandstone of Caithness. This little fossil, barely reaching 60 mm in length, has been a palaeontological conundrum since its first description by Traquair (1890); Dean (1904 : 425) remarks '*Palaeospondylus*, like Gloster, seems to have been born to bite the world'. Two Caithness men, Alexander and Marcus Gunn, 'delivered' *Palaeospondylus* into the scientific world by bringing it to the attention of Traquair. Their collecting efforts at Achanarras were recognized by Traquair who named it after them. *Palaeospondylus* has certainly had a 'bite' at many palaeontologists and zoologists, who have reacted by referring it to one or other of the many fish groups or, in some cases (Gill 1896; Dean 1898, 1900), to specially-erected classes or subclasses. When first described *Palaeospondylus* was regarded as an agnathan and this opinion received some initial consensus (Traquair 1890, 1893*a*, 1893*b*, 1894, 1897; Howes 1892; Woodward 1892, 1898; Dean 1895; Stensiö 1927; Bulman 1931; Ayers 1933; White 1935). This consensus was challenged on numerous occasions. Sollas & Sollas (1903) suggested it to be an elasmobranch. Kerr (1900) and Miller (1930) compared it to a larval

dipnoan, Dawson (1893) to a larval amphibian, Kyle (1926) to a larval herring, Dean (1904) to a holocephalan, and Jarvik (1980) regarded it as a larval *Osteolepis.* Huxley, it is said (Dean 1900), thought it to be a larval *Coccosteus* while Dean (1896, 1898, 1900) and Abel (1912) regarded it as a larval arthrodire. Finally, Moy-Thomas (1940) crystallized its placoderm relationships by suggesting it to represent a stegoselachian (a naked placoderm). Most modern text books (e.g. Parker & Haswell 1963, Romer 1966) deal with *Palaeospondylus* as an appendix to the placoderms.

Customarily, uncertainty about relationships of fossils arises from material which is poorly preserved or scanty, or both. But *Palaeospondylus* is known by, literally, thousands of specimens, almost all of which have been found at a single slate quarry on Achanarras Hill where it is distributed through several beds (Rayner 1963). At least one specimen was found in contemporaneous strata at Niandt (Traquair 1909) and a further example in the Sandwick Fish Bed at Cruaday Hill, Orkney (Trewin 1976). The Museum collections contain some 450 specimens. It is true that many are poorly preserved, leading Traquair (1890 : 485) to describe the head as a 'flat crushed mass of bony bars'. Other specimens, however, are preserved almost as well as other representatives of the Achanarras fish fauna (*Coccosteus, Homostius, Cheirolepis, Cheiracanthus, Mesacanthus, Rhadinacanthus, Diplacanthus, Pterichthyodes, Dipterus, Osteolepis, Glyptolepis*), the relationships of which have rarely been in doubt. *Palaeospondylus* has also been the subject of various preparation techniques, examples of which are in the Museum's collections. Sollas & Sollas (1903) used *Palaeospondylus* as one of their first experimental materials to produce wax-plate reconstructions (P.9856, P.9859–61). Bulman (1931) produced whole mount preparations (P.16120–5) and one specimen (P.22393) has been prepared by the acid transfer technique of Toombs & Rixon (1950). So the plea that the material is poor or insufficient fails in this case.

We suggest, instead, that the problem with *Palaeospondylus* is one generally inherent in fossils: that is, they are data 'in search of interpretation' (Nelson 1978 : 329). There are three main aspects to this problem. The first is incompleteness, in the sense that only the hard parts or a limited amount of the soft parts are preserved, thus reducing the amount of comparative information available for interpretation. Secondly, 'a fossil is meaningless until it can be interpreted in the light of a Recent model' (Patterson 1977 : 621). Finally a fossil is, by its very nature, in danger of being furnished with an ancestral status by over-zealous palaeontologists. The problems posed by *Palaeospondylus* fall into all three categories. The last-mentioned area was particularly characteristic of the early studies of *Palaeospondylus,* as the following remarks made by Dean (1904) show: 'For if the remains of *Palaeospondylus* are so poorly preserved that they cannot be definitely described, why do we continue to add papers to the troublesome literature? The only possible excuse 'is that the creature is seductive, full of suggestions as to the origin of the gnathostomes, and the mode of evolution of the jawless vertebrates.'

We shall begin by examining the earliest theories of the relationships of *Palaeospondylus* with the agnathans. Traquair (1890) noted the similarity in the shape of the head between *Palaeospondylus* and *Myxine* and, considering the period in which Traquair was working, it is not surprising that a relationship between the two should have been suggested. Toward the end of the nineteenth century palaeontology, through its concern with time, was beginning to emerge as the 'authority' on questions of phylogeny. Darwin predicted that, were the fossil record more carefully examined, progenitors of modern groups and links between groups would be found. So, one searched the rocks for suitably primitive and stratigraphically suitable candidates. *Palaeospondylus* was judged to be such an approximation to an ancestor of modern agnathans or, more specifically, to myxinoids (Traquair 1890; Bulman 1931). *Palaeospondylus* is naked like modern agnathans and was originally thought to have no jaws or fins. Its nakedness made it a better candidate than other jawless vertebrates—the heavily armoured heterostracans and osteostracans.

Several characters have been used to suggest relationship between *Palaeospondylus* and Recent agnathans: 1 – no jaws (Traquair 1890, 1893a, b, 1894; Stensiö 1927); 2 – no limbs (Traquair 1890, 1893a, b, 1894, 1897; Woodward 1892; Stensiö 1927; Bulman 1931);

3 – cirri surrounding a circular opening at the anterior end of the head, interpreted as a mouth (Woodward 1892; Traquair 1893a) or a nasal opening (Traquair 1893b, 1894; Stensiö 1927; Bulman 1931); 4 – single median recess at the anterior end of the cranium, interpreted to house a single nasal organ (Woodward 1892; Traquair 1893b; Stensiö 1927; Bulman 1931); 5 – V-shaped branchial pouch supports behind the head (Bulman 1931); 6 – dichotomized radials (often incorrectly referred to as fin rays) in caudal region (Traquair 1894); 7 – protocercal tail (Traquair 1893a, b, 1894, 1897); 8 – no discrete ossifications in the braincase (Traquair 1894).

Characters 1 and 2 are primitive, present in any non-gnathostome, and are not therefore agnathan characters any more than they are echinoderm or nematode characters. If the 'mass of bony bars' lying on the (presumed) ventral surface are not evidence of visceral arches then what are they? Three interpretations have been offered; that they are labial cartilages (Woodward 1892), that they are, in fact, ridges on the underside of the neurocranium and represent interbranchial ridges similar to those in cephalaspids (Stensiö 1927), or that they are remains of various cartilages supporting the tongue as in myxinoids (Bulman 1931). Most authors agree, as do we, that the 'bony bars' are visceral structures and that many are free or articulate with the braincase. This would seem to rule out any comparison with either lampreys or hagfishes, in which the visceral skeleton is unjointed and continuous with the neurocranium. Only gnathostomes show a jointed visceral skeleton which articulates with the neurocranium.

Character 3 has been commonly used for suggesting agnathan relationships, particularly with myxinoids. The more popular interpretation is that the 'cirri' (rostralia) surround a circular opening which represents a single nasal opening. Only hagfish, amongst agnathans, have a series of rostral cartilages (of different lengths) reaching in front of the nasal region. *Myxine* also has a row of cartilaginous rings around the nasal tube (Cole 1909 : fig. 1). Moy-Thomas (1940) examined several well-preserved specimens (P.22394, P.22401, P.22410) and found that considerable variation exists between individuals in the size and, to a lesser extent, the number of 'cirri'; he suggested that these together represented a fenestrated capsule(s). We would concur with this interpretation.

As to character 4, a median recess at the anterior end of the cranium is found in a variety of craniate embryos and is not an agnathan character. Character 5 is an interpretation of structures which have been otherwise interpreted as pectoral girdles and/or fins (Moy-Thomas 1940; Dean 1896). Character 6 is also found in elasmobranchs and lungfishes (Fürbringer 1904) and character 7 was shown to be a mistaken observation (Traquair had restored the tail upside down). The tail is now regarded as being asymmetrical with a slightly larger lower lobe. In any event, a protocercal tail is found in Recent lungfishes (Miller 1930).

Character 8 is difficult to evaluate since the nature of the preserved material is not clear. Microscope sections show no structure and the chemical composition, like that of other fossils from Achanarras, 'now consists of coal' (Sollas & Sollas 1903 : 273). The skeletal material has been interpreted as bone (Traquair 1890), or as calcified cartilage (Traquair 1839a), but there is no evidence to favour either of these suggestions.

So, in our opinion, not one piece of evidence has been produced suggesting *Palaeospondylus* to be an agnathan and interpretation on an agnathan model (hagfish or lamprey) is not justified. The presence of ring centra would also militate against agnathan relationships. Hagfish have no chondrification or ossification around the notochord, lampreys have cartilaginous dorsal arcualia and the only evidence of a vertebral column in ostracoderms is the impressions of (presumably) neural arches in some cephalaspids (Janvier 1980). The presence of ring centra in *Palaeospondylus* as an agnathan ancestor was explained by assuming that absence of skeletal ossification is a derived condition of Recent agnathans. We do not wholly share this view. Hagfishes, which we regard as the sister group of lampreys and gnathostomes (Løvtrup 1977; Hardisty 1979; Janvier & Blieck 1979), never possessed bone or paired fins in their history. This might also be true of lampreys, in which case we would regard lampreys and anaspids as the sister group of osteostracans and gnathostomes (Janvier, personal communication).

We accept that *Palaeospondylus* has visceral arches, albeit they are difficult to interpret, and agree with Moy-Thomas (1940) that there is evidence for both pectoral and pelvic fins. We therefore believe that *Palaeospondylus* is either the sister-group of gnathostomes or a member of some gnathostome subgroup. Several suggestions have been offered (p. 134). Sollas & Sollas (1903) considered it to be an elasmobranch but one that 'proceeded in its subsequent development along an independent course, losing its limbs, if it ever possessed them, and acquiring a highly organised vertebral column, homoplastic in character with that of cyclo-spondylous Selachians' (1903 : 290–291). The main reason given by these authors for elasmobranch affinities is the general similarity in the shape of the head: the eye is situated immediately in front of the otic capsule, and there is a saddle-shaped ledge on the ventral surface of the neurocranium, marking the position of the pituitary body. We find nothing particularly elasmobranch about these features: we cannot confirm the presence of a 'saddle-ledge' but note that the ventral profile of *Squalus* is very similar to that of larval *Acipenser* and *Neoceratodus* (de Beer 1937). The particular shape of the ventral profile may thus be no more than a general early ontogenetic feature of gnathostomes. Dean, in perhaps light-hearted mood (1904 : 425), suggested that *Palaeospondylus* is a holo-cephalan. He based this suggestion on four characters: continuous dorsal fin (no evidence), protocercal tail (incorrect observation), ring vertebrae (known elsewhere – chondrichthyes, larval teleosts, sarcopterygians) and a huge head.

Moy-Thomas regarded *Palaeospondylus* as an adult and to be a stegoselachian, a group of placoderms in which there is little development of armour – Stensioellidae and Rhenanida. He chose to make comparisons with these but also with acanthodians, presumed close relatives of placoderms (Watson 1937), and arthrodires. Moy-Thomas's model was therefore a placoderm + acanthodian morphotype (an aphetohyoidean, established by Watson as a grade group). Moy-Thomas mentioned eight characters to support his argument, citing precedents within selected placoderms and acanthodians: 1 – heterocercal tail; 2 – anterior position of the pelvic fins (like *Pseudopetalichthys* and *Rhamphodopsis* – a ptyctodont); 3 – ventral mouth and small size of lower jaw; 4 – palatoquadrate ossified in more than one piece in which the 'tauidion' (Sollas & Sollas 1903) represents the medially united anterior ossifications; 5 – ring-like centra (*Gemuendina* and *Pseudopetalichthys*); 6 – short occipital region (like *Jagorina,* but most placoderms have long occipital regions); 7 – well-developed rostral region (like *Nessariostoma*); and 8 – hyomandibular not supporting jaws (but the hyomandibular is involved in jaw suspension of most placoderms (Miles 1971) and the jaw suspension of acanthodians is known to have a suspensory hyomandibular (Miles 1973)). Once again, all these characters can be matched outside placoderms and acanthodians and we find no placoderm characters in this list.

Jarvik (1980) has recently suggested that *Palaeospondylus* is a larval *Osteolepis*. His argument is in two stages. He first notes the similarity between *Palaeospondylus* and anuran tadpoles (presence of ossified ring-like centra and external shape of the tail). He then argues (1980 : 218) that ' . . . because osteolepiforms have been shown to be close to the ancestry of the Anura it is tempting to suggest that *Palaeospondylus* may be a larva of *Osteolepis macrolepidota,* an osteolepiform which is also common in the flagstones at Achanarras'. To this we would make three comments: the similarities between anuran tadpoles and *Palaeospondylus* are not unique; immediate relationship between anurans and osteolepi-forms is not beyond doubt (Rosen *et al.* 1981); *Osteolepis* is very rare at Achanarras, there being only approximately 16 specimens known (Trewin, personal communication).

One of the most distinctive structures of *Palaeospondylus* are the so-called 'post-occipital lamellae' which are readily visible and which, we believe, offer a clue about relationships. The 'post-occipital lamellae' are represented by a pair of rods which lie on either side of the anterior centra. Amongst living fishes there are very few comparable structures. Moy-Thomas regarded them as part of the branchial arch series although 'why they are so much enlarged is still a mystery' (1940 : 401). In this he finds agreement with Dean (1896) and Sollas & Sollas (1903). Other interpretations include: parachordals (Jaekel 1927), pronephric lamellae of cephalaspids (Stensiö 1927), the posterior lingual cartilage of a myxinoid

(Bulman 1931), a rudimentary dorsal shield (Woodward 1892), elements of a shoulder girdle (Kyle 1926) or a cranial rib of a dipnoan (Kerr 1900).

The last interpretation seems particularly promising to us since the comparable structures in Recent dipnoans are so similar in shape and position, and are distinctively large. The structures in question have rounded, presumably articulatory, heads (Fig. 2B) and always lie against the posterior edge and slightly on the ventral surface of the neurocranium. This was therefore their position in life. They are associated (? articulated) with smaller, angulated structures (branchial arches – Sollas & Sollas 1903, Moy-Thomas 1940), which may be interpreted as occipital neural arches. Our comparisons of cranial ribs seem most favourable with *Protopterus* and *Lepidosiren* (Agar 1906 : figs 9, 16).

We agree with Kerr (1900, 1919) and Miller (1930) that these enlarged structures are cranial ribs and this allows us to interpret *Palaeospondylus* as a lungfish. Our interpretation of the visceral structures is given in Fig. 2B and is based on comparisons with the illustrations of lungfish larvae provided by Agar (1906), Kerr (1919) and Fox (1965). The many specimens of *Palaeospondylus* show considerable variation but we have found it impossible to relate differences in structure to absolute size. This is chiefly because the several visceral elements are very difficult to interpret; it is not easy to decide where there are points of articulation or, in some cases, whether an element is separate or not. Diagenesis must have affected such an obviously delicate animal. For this reason we do not intend to describe the skull. Instead we will simply point out several important areas of agreement and disagreement between the restoration given here and those offered by Moy-Thomas (1940 : figs 2, 4). We agree that the 'rostralia' are expanded distally and that they may be fused distally, thereby forming together a fenestrated capsule. The resemblance between this and (partially macerated) nasal capsules of *Lepidosiren* was noted by Kerr (1900) and Miller (1930 : fig. 5). The 'tauidion' (Sollas & Sollas 1903) is a prominent structure which we compare to a dipnoan vomer. We agree that the paired elements which lie beneath the otic capsules and converge anteriorly are ceratohyals (always large in dipnoans and urodeles), and that the small unpaired element immediately behind the anterior ends of the ceratohyals is a basibranchial. We disagree with Moy-Thomas over the interpretation of those visceral elements anterior and lateral to the otic capsule. These have been the most problematical elements, interpreted differently by Sollas & Sollas (1903), Bulman (1931) and Moy-Thomas (1940). We believe that the 'hyomandibular' is nothing more than the thickened edge along the anterolateral margin of the otic capsule and may be compared to the otic process of the palatoquadrate; that the 'gammation' and posterior trapezial bar of Sollas & Sollas (1903) compose a single element (specimen P.22392) representing the quadrate region of the palate; and that the 'anterior trapezial bar', 'pregammation' and perhaps the 'hemidome septum' are palatal elements. Since the last-mentioned elements are the most variable they might represent developing tooth ridges (cf. Kerr 1919 : fig. 164c).

Like Moy-Thomas, we consider that the palatoquadrate is fused to the neurocranium and find it interesting that Moy-Thomas chose to make his comparison of the skull with the urodele *Hynobius*. Identification of the lower jaw is difficult. It is possibly represented by the outer curved element, representing a Meckelian ossification/chondrification which forms the outer edge of the 'hemidome'. This is expanded posteriorly and articulated with that element identified here as the quadrate. Anteriorly it curves to meet its antimere immediately in front of the vomer, as it would in a dorsally flattened head.

Moy-Thomas rejected dipnoan affinities of *Palaeospondylus*, chiefly on the ground that he considered it to be an adult. He noted the existence of centra and the advanced degree of ossification. The nature of the skeleton has never been established beyond the fact that it is chemically like coal. Centra are known in larval teleosts—indeed, this was one of the reasons that led Kyle (1926) to consider it as a larval herring. If *Palaeospondylus* were an adult we find it unlikely that fin rays would be absent, that any trace of dermal covering would be absent, that the girdles would be such insignificant structures and that the neurocranium would be so open and trough-like dorsally. These features are those of larvae.

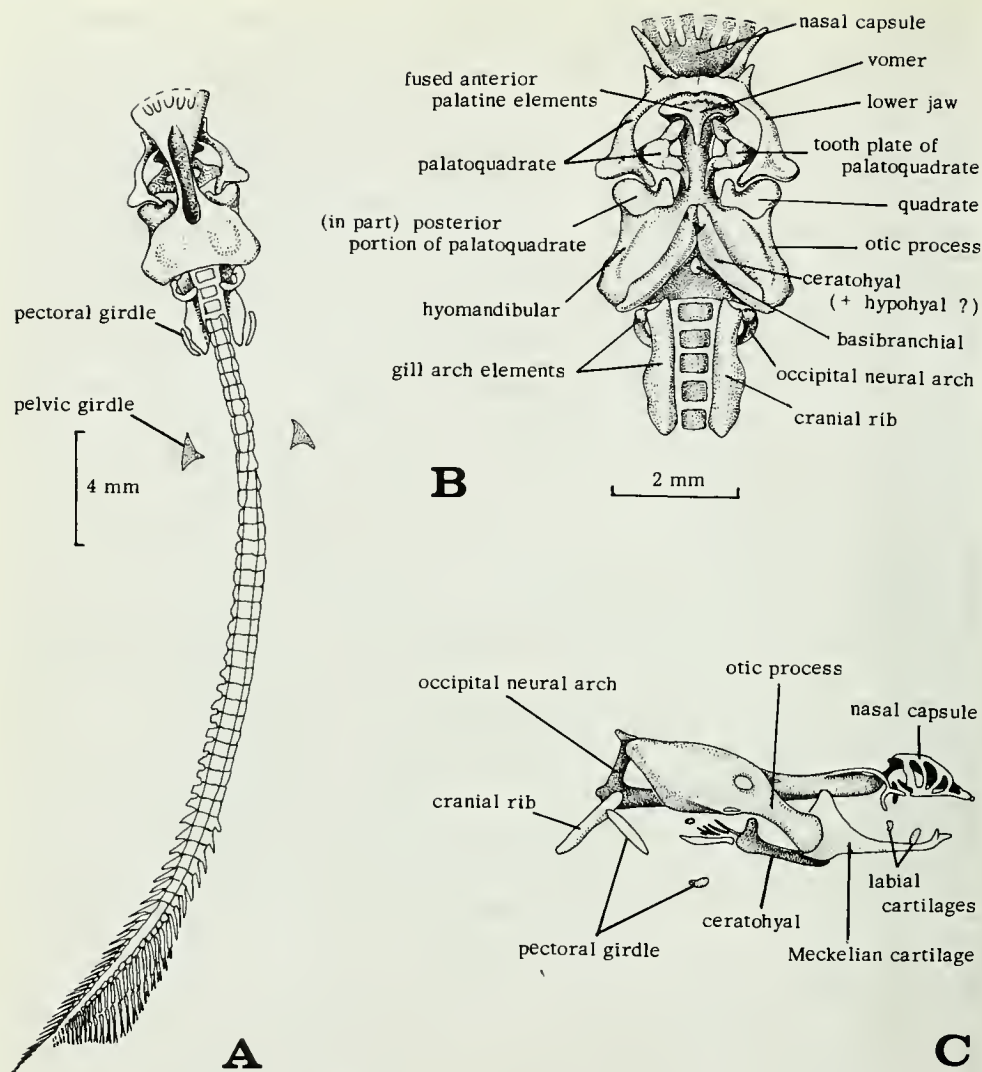The logical conclusion is that *Palaeospondylus* is a larval *Dipterus*, the only lungfish

Fig. 2   A, reconstruction of *Palaeospondylus*. Skull in dorsal view, posterior portion of trunk and tail twisted to appear in right lateral view. Based on Moy-Thomas (1940 : fig. 7), skull redrawn. B, restoration of the head of *Palaeospondylus* in ventral view. Labelling on right-hand side represents our interpretation, that on the left Moy-Thomas's. C, *Lepidosiren*, stage 38. Reconstruction of the head of the embryo in lateral view, tooth plates omitted. After Agar (1906 : pl. 3, fig. 16).

present in the fauna. Centra are not normally recorded for *Dipterus* but Jarvik (1952) records them and specimen P.10613 shows centra in at least the tail region. The tail of *Dipterus*, unlike that of many Dipnoans, is also asymmetrical. We can, however, suggest no morphological character which would refer it specifically to *Dipterus*.

We recognize that our interpretation of *Palaeospondylus* fossils, even at such an elementary level as deciding whether a structure is fused or articulated, is governed by our

initial choice to use a particular model. Such is the nature of palaeontology. The difference between our attempt and those of most other workers who have considered *Palaeospondylus* (with the exception of Kerr) is that we have attempted to identify a synapomorphy with a Recent group, rather than rely on obviously primitive features (as did Traquair and Bulman), features which are not characters of groups (Moy-Thomas) or use other fossil groups as models (Stensiö). We leave *Palaeospondylus* as larval dipnoan to 'seduce' or to 'bite' other palaeontologists.

Jamoytius and *Moythomasia*

Two genera of fossil fishes have subsequently been named after Moy-Thomas. The first was *Jamoytius* by E. 1. White in 1946 and the second *Moythomasia* by W. Gross in 1950.

Genus *JAMOYTIUS* White, 1946
Fig. 3

DIAGNOSIS. See White 1946.

TYPE SPECIES. *J. kerwoodi* White 1946.

REMARKS. When first described by White (1946 : 93) the naked *Jamoytius* was considered not only as a likely ancestor for amphioxus but also for the Craniata. White consequently erected the new order Euphanerida to incorporate it. These suggestions, however, did not meet with universal favour and *Jamoytius* was subsequently regarded as a larval thelodont by Wängsjö (1952 : 566) and as an anaspid by Robertson (1953 : 734). Smith (1957 : 394) and Stensiö (1958 : 239) concurred with Robertson and suggested that 'the carbonized remains of the body muscles (myocommata)' were scales. Tarlo (1960 : fig. 5), after a re-examination of the holotype, not only confirmed both Smith's (1957) and Stensiö's (1958) contentions but also claimed the presence of ridge scales. More recently Newth (*in* Young 1962 : 128) has suggested it to be the ammocoete larva of an ostracoderm and Wickstead (1969 : 422) that it corresponded to a metamorphosing amphioxus. Ritchie (1960, 1968) has published accounts based on new material, in which he claimed to have confirmed the presence of scales.

Jamoytius kerwoodi White 1946

1946 *J. kerwoodi* White : 89.
1960 *J. kerwoodi* White; Tarlo : 113, fig. 5.
1960 *J. kerwoodi* White; Ritchie : 647, fig. 1.
1968 *J. kerwoodi* White; Ritchie : 26; pls 3–6.

DIAGNOSIS (emended). A naked cyclostome with diphycercal tail and branchial basket.

REMARKS. We cannot find any trace of scales on the specimens examined (BM(NH) and Royal Scottish Museum). Furthermore, the carbonized remains bear no resemblance to anaspid scales. The so-called scales seen by Ritchie (1960, 1968) were only observed by him after the specimens had been treated. No such structure is visible on any specimen we have examined and we suggest that both Tarlo (= Halstead) and Ritchie were mistaken in their observations. Futhermore, no good evidence has been presented against regarding the segmental structures as the remains of body muscles. In no specimen is there anything more than carbonized remains and occasionally a rather amorphous, tarry, surface structure.

There is likewise no evidence for a lateral fin fold either on the holotype (cf. White 1946 : fig. 1) or on RSM 1966. 3.1 (cf. Ritchie 1968 : pl. 4).

In our estimation the fossil looks very similar to the present-day lamprey and like it has a branchial basket (Fig. 3) with horizontal struts and a diphycercal tail. The branchial basket has no more than seven openings and the appearance of paired structures (eyes) and an annular cartilage argues against it being a larval amphioxus.
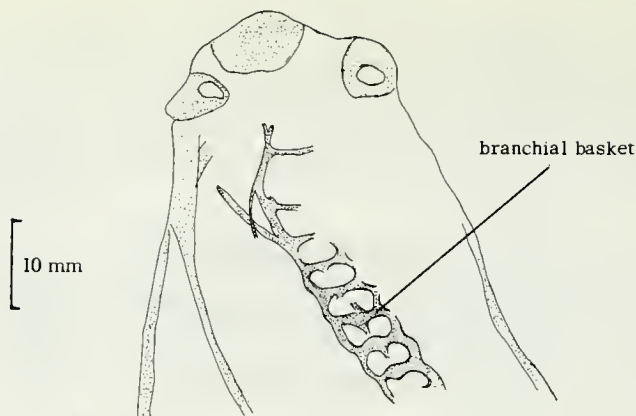
Fig. 3 *Jamoytius kerwoodi* White. Sketch of anterior portion of head as preserved in BM(NH) P.47787, showing the lamprey-like branchial basket.

<div align="center">

Genus *MOYTHOMASIA* Gross, 1950

[= *Aldingeria* Gross 1942 : 431, *non* Moy-Thomas 1942]

</div>

DIAGNOSIS. See Gross, 1942 : 431.

TYPE SPECIES. *M. perforata* (Gross).

REMARKS. The name *Aldingeria* was first used by Moy-Thomas in October 1942 for a Carboniferous palaeoniscid from East Greenland. Two months later in December of that year the same name was used by Gross (1942 : 431) for a very different palaeoniscid from the Upper Devonian of the Baltic. When Gross realized that *Aldingeria* Moy-Thomas took priority over *Aldingeria* Gross he replaced his genus with the name *Moythomasia* (Gross 1950 : 145) in honour of the British palaeontologist.

When first described by Gross, *Moythomasia perforata* appeared to be just another palaeoniscid. Fortunately, however, this genus also occurs in the calcareous Devonian rocks of Australia (*M. durgaringia* Gardiner & Bartram 1977) and it has turned out to be far more interesting than ever Gross could have imagined.

<div align="center">

Moythomasia durgaringia Gardiner & Bartram 1977

</div>

DIAGNOSIS. See Gardiner & Bartram 1977 : 238.

REMARKS. This species closely resembles *Mimia toombsi* Gardiner & Bartram, from which it only differs significantly in having a short ascending process.

Moythomasia is regarded as the sister-group of the Actinopteri (Rosen *et al.* 1981), sharing with them a differentiated propterygium in the pectoral fin, a pelvic fin exclusively supported by preaxial radials, fringing fulcra, ganoid scales, acrodin caps on marginal teeth, an endopterygoid, a dentary with a sensory canal and the absence of the jugal/infraorbital canal junction. *Moythomasia* and *Mimia* do not possess a stem to the parasphenoid, or a process on the post-temporal. The ventral fissure and otico-sphenoid fissures were cartilage-filled and not completely bridged by dermal bone (i.e. the parasphenoid), and the lateral occipital fissure is perichondrally lined in both. All of these features suggest that these two genera are the sister-group of all other actinopterygians, with the exception of *Cheirolepis* which lacks acrodin caps on its teeth and fringing fulcra, and *Polypterus* which lacks fulcra and ganoid scales.

Conclusion

During Moy-Thomas's life-time significant advances were made in our understanding of fossil fishes. New methods of examining fossils were introduced, including acid preparation, the use of fine dental hammers, serial sectioning and microscope examination under liquids of varying refractive indices. And there was also a concomitant influx of literature. Perhaps Moy-Thomas's most important contribution was to summarize this information in the light of his own research, and to embody it in his book *Palaeozoic Fishes* (1939). Beyond this, however, he was typical of those numerous individuals who rightfully use this National Museum. We hope that the next hundred years will produce as many fruitful collaborations as the last.

Below, we print a complete bibliography of Moy-Thomas's contributions.

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